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## New Species of *Passiflora* Subgenus *Plectostemma* (Passifloraceae)

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**ABSTRACT.** Four new species are described, one with two distinct subspecies: *Passiflora* (sect. *Cieca*) *juliana*, *P.* (sect. *Cieca*) *xiikzodz* subsp. *xiikzodz* and subsp. *itzensis*, *P.* (sect. *Pseudodysosmia*) *oaxacensis*, and *P.* (sect. *Xerogona*) *escobariana*. *Passiflora juliana* appears to be the closest relative of *P. viridiflora* Cavanilles, a species that traditionally has been segregated as a distinct section or subgenus.

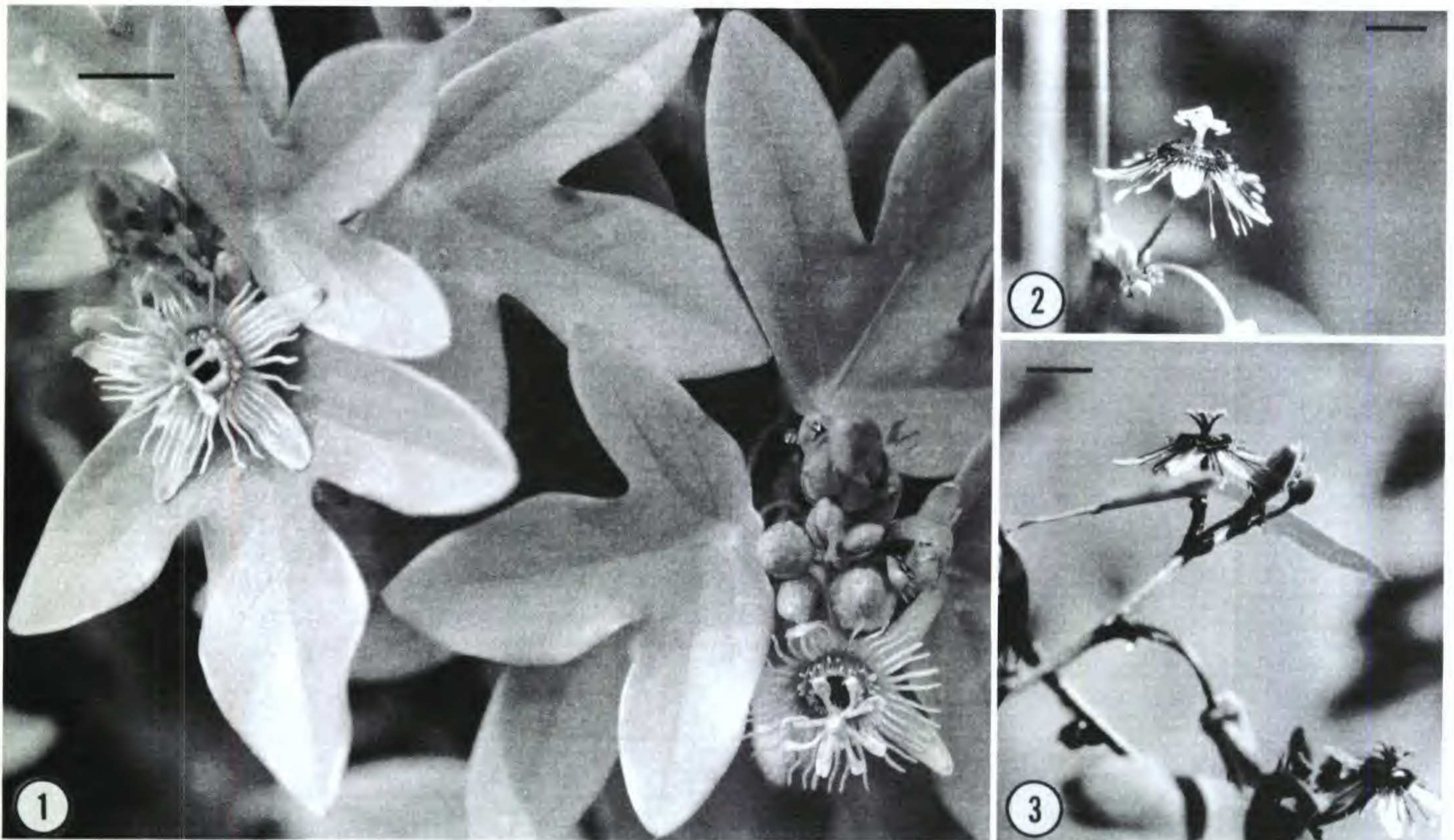
Revision of Mexican, Central American, and Colombian collections of passionflowers is yielding numerous undescribed species, especially among the small-flowered subgenus *Plectostemma* Masters. Apetalous passionflowers, found only in subgenus *Plectostemma*, form a group of about 18 closely related species called section *Cieca* (Medikus) DeCandolle. This section is most diverse and common in northern Mesoamerica and southern Mexico, with a radiation of relatives of *P. suberosa* Linnaeus in the Caribbean. There are at least two other apetalous species in other sections, but these occur independently elsewhere in the subgenus. The following two new species are in section *Cieca*.

***Passiflora juliana*** J. MacDougal, sp. nov. **TYPE:** Mexico. Michoacán: Mun. Coahuayana, high point on coastal road (Hwy. 200) between San Telmo and San Juan de Lima, 70 m, 2 Nov. 1979, J. M. MacDougal 492 (holotype, DUKE; isotypes, CAS, CHAPA, DUKE, ENCB, F, GH, IBUG, MICH, MO, MEXU, NY, TEX, US, XAL). Figure 1.

*Passiflora* ad sectionem *Ciecam* pertinens, scandens; stipulae (3-)5-12(-15) mm latae; petioli in parte media biglandulosi; folia peltata glandulosa trilobata, lobis acutis vel plerumque obtusis vel subrotundatis, marginibus integris; pedunculi ebracteati; stipes floralis 2-4 mm longus; petala nulla; coronae filamenta 2-seriata, filamentis exterioribus 6-8 mm longis, viridiflavis; operculum plicatum; androgynophorum 4-5 mm longum; ovarium glabrum; fructus baccatus atropurpureus; semina 3.7-4.1 mm longa, reticulatim foveata.

Vine (1.5-)2-3 m, minutely to microscopically puberulent throughout at the shoot tip with antrorsely appressed curved trichomes 0.08-0.12 mm long, except adaxial surface of laminae and stipules glabrous; plant glabrescent below. Stems ca. terete

to elliptical, often reddish, with minute appressed trichomes. Stipules (6-)10-20(-23) × (3-)5-12(-15) mm, foliose, asymmetrically obovate (to ovate), acute; petioles 1-4 cm, 2-glandular (0.25-)0.3-0.6 the distance to the apex, the nectaries 2 × 1.0-1.5 mm, saucerlike, fleshy, sessile or narrowed at the base; laminae 3.5-10 × 6-16 cm, peltate (3-)5-15 mm from margin, entire, sometimes variegated as juveniles, the variegations scattered as small patches of white, this rarely retained at reproduction, depressed obovate to widely depressed obovate in general outline, 3-lobed 0.40-0.72 the distance to the peltate base, 5-7-veined, glabrous and often matte adaxially, glabrescent and glaucous abaxially, the lobes elliptic or more usually obovate (or the central widely obovate), apices obtuse or sometimes rounded, the central lobe narrowed at base, the angle between the lateral lobes (80°-)110°-160°; juvenile leaves more deeply lobed with narrow segments; laminar nectaries present as 2-6(-10) sessile submarginal glands distal to lateral veins, (one juvenile plant seen with 1 gland per lateral lobe also proximal to lateral veins), glands 1 mm or less in diameter, (2-)3-5 mm from margins. Peduncles (1)2 per node, 7-20(-27) mm long, uniflorous, green (one individual seen with branched peduncles, 1-2(-3)-flowered); bracts absent; conspicuous inflorescences 5-19 cm long often present as condensed terminal shoots with aborted laminae, the petioles and their nectaries still present. Flowers borne facing above the horizontal to nearly vertical, yellowish green, with a hardly detectable slightly sweet odor, open and receptive from late morning past midday; stipe 2.0-4.0 mm; hypanthium ca. 7-8 mm diam.; sepals (9-)10-12 × 4.0-6.0 mm, light green or yellowish green, with no apical projection; petals absent; coronal filaments in 2 series, the outer ca. 28-48, 6-8 mm long, tapering to points at tips, slightly laterally compressed, opening to or slightly more than 180°, light greenish yellow to light yellow apically, unmarked or with a mere flush of purplish or reddish spots adaxially at base, the inner 3.2-3.7 mm, erect to slightly spreading, greenish yellow and sometimes with a tinge of purplish at very base, capitellate; operculum 2 mm long, membranous, plicate, greenish yellow; limen floor violet to dark



Figures 1-3. —1. *Passiflora juliana* J. MacDougal, with beginning of terminal inflorescence (MacDougal 492GR). Scale bar = 1 cm. —2. *Passiflora xiikzodz* subsp. *xiikzodz* (MacDougal 4677). Scale bar = 1 cm. —3. *Passiflora xiikzodz* subsp. *itzensis* (MacDougal 4633). Scale bar = 1 cm.

purple, its raised edge white or purplish and slightly inclined toward androgynophore; androgynophore (4.0–)4.5–5.0 mm long, whitish or pale green with the purple coloring of the limen ascending only a few mm at base, or purple nearly to the apex; staminal filaments free 3.0–3.5 mm, light greenish, anthers 3.3–4.0 mm long, light greenish, not spotted or marked; pollen light yellow; ovary 2.4–3.0 × 1.5–2.0 mm, ellipsoid, glabrous, green; styles 4.0–5.0 mm total length, including stigmas, the stigmas 1.5 mm diam., light green. Fruit 1.3–2.5 × 1.3–2.0 cm, depressed globose to slightly ellipsoid, sometimes somewhat trigonal-round in cross section, estipitate, bluish black with a white bloom, thus appearing dark gray-blue, exocarp mildly fruity, neither sweet nor sour; arils clear, with a distinct white line (funiculus) on the side, close fitting, ± tasteless; seeds 3.7–4.1 × (2.2–)2.5–2.9 mm, slightly campylotropous, the chalazal beak slightly inclined toward the raphe, reticulate-foveate with 11–15(–18) foveae per side. Germination epigeal. Chromosome number  $2n = 12$ .

*Distribution and habitat.* *Passiflora juliana* is restricted to the coast and coastal plain of southwestern Mexico. It is not uncommon near rocky cliffs overlooking the Pacific Ocean and in the coastal forest in the hills and away from the coast. Collectors' notes give the following habitats: common on road-cut banks and cliffs in sun; on rocky ledge

of arid slope with low scattered trees; in shrubs; wooded plain of *Crescentia-Juliania* savanna; selva baja caducifolia; bosque tropical caducifolia; abundant on shrubs on low mountain summits with deciduous woodlands; thickets and rocks at cliff-tops; roadside thickets; grows best in sunny areas; dappled shade of secondary forest of low stature. In Michoacán I found it associated with or near *Passiflora holosericea* Linnaeus, *P. goniosperma* Killip, *P. mexicana* A. L. Jussieu, and *P. filipes* Benth.

*Paratypes.* MEXICO. COLIMA: Mun. Tecoman, N of Tecoman, 3.9 mi. NE on Hwy. 110 from jct. of road to Tecoman (Hwy. 200), 30 Oct. 1979 (fl), MacDougal & Miley 486 (CAS, CHAPA, DUKE, ENCB, IBUG, MEXU, MICH); 15 mi. SE of Tecoman, near Cerro de Ortega, 0–50 m, 9 Dec. 1959 (fl), McVaugh & Koelz 1615 (MICH); 7 mi. N of Santiago, rd. to Durazno, Jalisco, via bridge over Río Cihuatlán, 200 m, 30 July 1957 (fl), McVaugh 15924 (MICH). JALISCO: 2 km by road E of Cihuatlán, 0–50 m, 8 Mar. 1970 (fl), Anderson & Anderson 6154 (MICH); 19°30'N, 105°03'W, 6 Jan. 1983 (fl), Lott 1701 (DUKE, MEXU); Mun. La Huerta, entrada a la vereda a las Piletas cerca de Rincón de Ixtlán, viejo camino a Nacastillo, 12 Aug. 1983 (fr), Lott 1832 (DUKE, MEXU); Mun. Cihuatlán, 2.8 mi. W on Hwy. 200, 4.2 mi. E of road to Barra Navidad, 10 Nov. 1979 (fl), MacDougal & Miley 507 (MO-spirit); Mun. La Huerta, Estación de Biología Chamela, 10 Dec. 1976 (fr), Magallanes 344 (DUKE, MEXU); 13 Dec. 1976 (fl, fr), Magallanes 364 (MEXU); high rocks above the Pacific Ocean, Rancho Paraíso, 10 km SE of Chamela, 20 m, 14 Feb. 1975 (fr), McVaugh 26277 (MICH). MICHOACÁN: Mun. Apatzingan, Tancitaro region, Mt. Apatzingan, 2,000

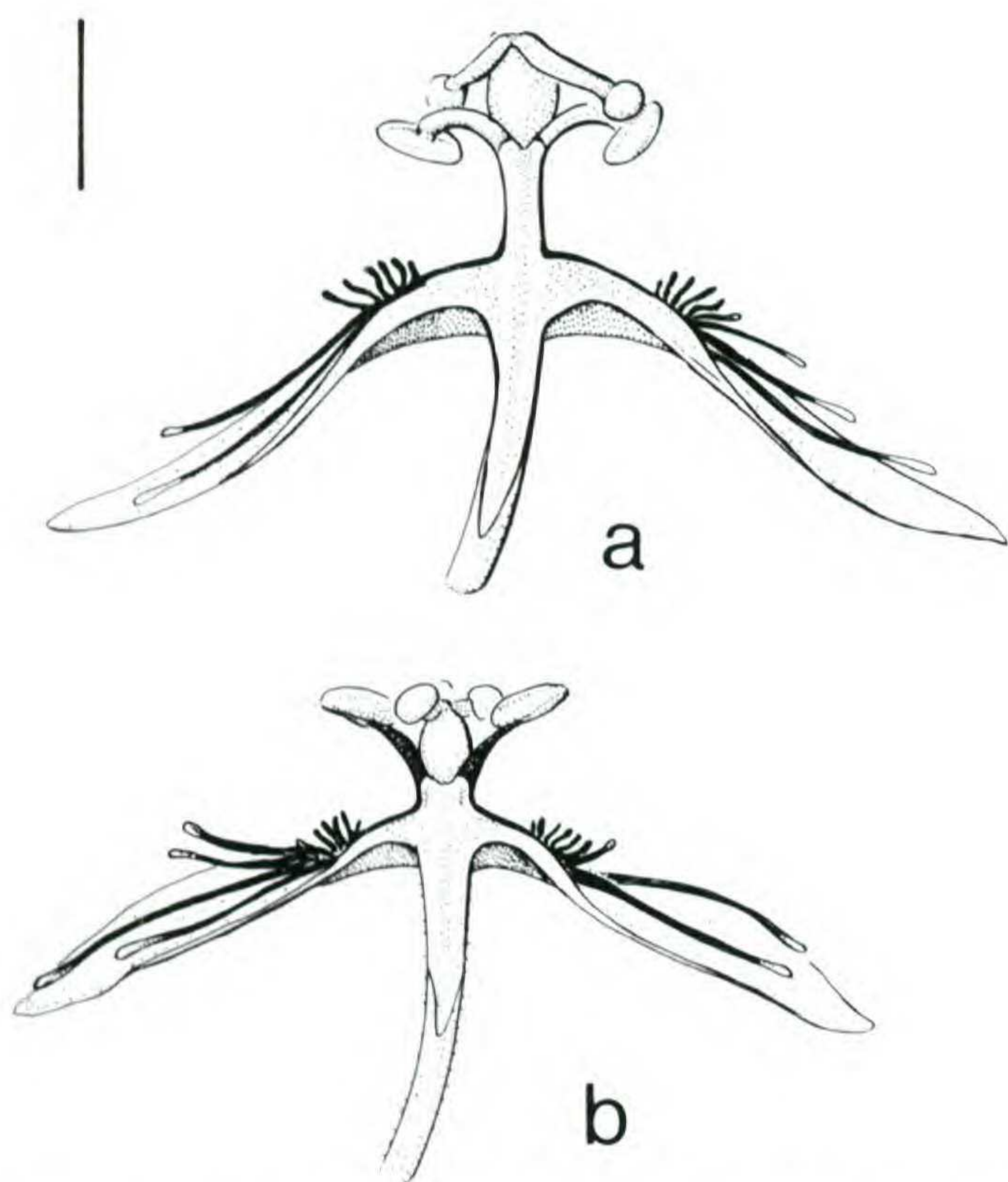


Figure 4. Diagram of floral cross sections of *Passiflora xikzodz* J. MacDougal. Scale bar = 5 mm. —a. *P. xikzodz* subsp. *xikzodz* (MacDougal 4677). —b. *P. xikzodz* subsp. *itzensis* (MacDougal 4633).

ft., 20 Aug. 1941, *Leavenworth & Hoogstraal 1717* (F); Mun. Coahuayana, 7.7 mi. SE from Río Coahuayana on Hwy. 200, 31 Oct. 1979, *MacDougal & Miley 489* (DUKE); Mun. Huetamo, 3 km al NW de Eréndira, sobre el camino a Carácuaro, 800 m, 6 Nov. 1977, *Rzedowski 35506* (ENCB).

*Passiflora juliana* very closely resembles *P. viridiflora* Cavanilles vegetatively, except that it has notably wide and foliose stipules and the stem is not as bright red. The length of the androgynophore is the main difference between the two: *P. viridiflora* has an elongate tubular flower, while *P. juliana* has the shallow-dish shape that is usual in the section and subgenus. Both inhabit similar habitats along the Pacific Coast of Mexico, with *P. juliana* to the north and *P. viridiflora* southward down the coast, from Acapulco to the Isthmus of Tehuantepec. The two species apparently are not sympatric, but the possible zone of contact has not been sampled. They are undoubtedly sister species.

*Passiflora viridiflora* is pollinated by hummingbirds in coastal Oaxaca (A. Lau, pers. comm.). The usual pollinator of *P. juliana* is unknown; my one morning of observation yielded only a single hurried visitor—a hummingbird. The floral structure of *P. juliana* suggests adaptation to a small or medium-sized insect.

The discovery of a passionflower that is clearly referable to section *Cieca*, but that very closely

resembles *P. viridiflora* (except for the bird-adapted flower), reinforces the placement of *P. viridiflora* in section *Cieca*, a position previously suggested by MacDougal (1983).

*Passiflora viridiflora* has been recognized as a distinct monotypic genus, *Synactila* Rafinesque, and at various infrageneric ranks within *Passiflora*, but the discovery of this new species with intermediate morphology confirms that *P. viridiflora* is not as distinct as once thought. The elongate flower probably merely represents a shift in pollinators.

*Passiflora juliana* has a conspicuous terminal inflorescence on older plants that consists of a condensed shoot with extremely reduced or aborted laminae. A short petiole remains at each node and the petiolar nectaries are well developed and active. The shoot of the inflorescence is not determinate, however, and vegetative growth with normal leaves and longer internodes often continues after weeks or months of blooming. This inflorescence is identical to those seen in the related species, e.g., *P. viridiflora* and *P. coriacea* A. L. Jussieu. Laminar nectaries are distal to the lateral veins except in one specimen, *Rzedowski 35506*, where single glands occur proximal to the main veins of each lateral lobe. Plants from Jalisco and Colima tend to have more laminar nectaries than the forms from Michoacán, with up to 8 or 10 per leaf. The type gathering consisted of several individuals growing adjacently. Branched peduncles, seen only in one individual of the type gathering (cf. isotype, DUKE), are to be considered an abnormal condition in this species. This character state is not shared with any other collection of *P. juliana*, nor with other species in section *Cieca*, except that it has been observed in certain races of *P. suberosa* (cf. *MacDougal 421*).

A few seeds from fruits on the type gathering were stored dry and clean for 2½ months, then sown. Germination was excellent within 10 days, and the seedlings were numbered *MacDougal 492GR*. In 1983 several of these seedlings were distributed to the horticultural trade in California and made available at the retail level in limited quantities. Less than 20 cuttings were distributed in the next decade, but clones are still available from several growers. The chromosome count was from *MacDougal 492GR* (Snow & MacDougal, in press).

*Passiflora juliana* appears to be self-incompatible, as no fruits were produced from over 50 controlled self-pollinations performed on *MacDougal 492GR* in the greenhouse. No fruits have been produced by autogamy during ten years of cultivation. Hybrids were produced from *492GR* on an extremely limited basis by MacDougal in 1982 by

crossing *P. juliana* with *P. trinifolia* Masters and *P. tenuiloba* Engelm. The several plants grown of these two crosses were variegated (chimera-type) and dwarfed like their smaller parents, but otherwise were essentially intermediate to the parental morphology. Hybrids flowered with normal-looking, intermediate flowers with abundant pollen; pollen viability or stainability has not been examined. Fertile vouchers of examples of these crosses are deposited at DUKE.

Dried leaf samples of *MacDougal* 492GR (as 492) were chromatographically screened by McCormick (1982) for flavonoids. Flavonol 3-*O*-glycosides but not *C*-glycosylflavones were detected. This is an unusual pattern in *Passifloraceae*, and was found in all of the species of section *Cieca* that contained any flavonoids, including *P. viridiflora* (McCormick, 1982).

Lacebugs and the butterfly *Heliconius charitonius* were important herbivores on *MacDougal* & Miley 486.

The species is named for Julianna Miley, my former wife and beloved companion during the Mexican and Guatemalan fieldwork of 1978 to 1980. Her enthusiastic assistance resulted in the discovery or re-collection of many species of passionflowers.

***Passiflora xiikzodz*** J. MacDougal, sp. nov. TYPE: Mexico. Campeche: Tuxpeña, [18°26'N, 90°06'W], 19 Jan. 1932, *Lundell* 1210 (holotype, MICH; isotypes, ARIZ, DS, F, GH, MICH, MO, NY, US, WIS—2 sheets, U). Figures 2–4.

*Passiflora* ad sectionem *Ciecam* pertinens, ad rupes calcareas scandens; stipulae 0.4–0.7 mm latae; petioli ad apicem biglandulosi; folia peltata glandulosa bilobata vel truncata vel raro trilobata, lobis lateralibus acutis vel raro acuminatis, marginibus integris; pedunculi ebracteati, stipes floralis 12–30 mm longus; petala nulla; coronae filamenta 5–7(–8)-seriata, filamentis exterioribus filiformibus 8–12 mm longis, pro parte maxima atropurpuris, ad apicem flavidis; operculum ad basim in denticulos lacera tum; androgynophorum nullus vel 0.5–4 mm longum; ovarium glabrum; semina ca. 4.3–5.5 mm longa, reticulatim foveata.

Vine ca. 1–3(–6) m, minutely to microscopically puberulent throughout with antrorsely appressed, curved blunt trichomes 0.08–0.12 mm long, and sometimes also straight, erect, capillary trichomes to 0.3 mm long, except the laminae glabrous or nearly so; plant glabrescent below. Stems subterete to obtusely subangular, ca. scabrous, minutely puberulent. Stipules (2.8–)3.5–6.5 × 0.4–0.7 mm, linear to linear-lanceolate; petioles 1–2(–3) cm, 2-glandular at or near the apex (or at least on the

distal ¼), 0–5(–10) mm from the apex, the nectaries 0.7–1 × 1.3–2 mm, saucerlike, fleshy; laminae (1.2–)1.5–7.5 × (3.5–)5–19 cm, peltate (2.5–)3–5(–10) mm from margin, entire, usually strongly variegated along main veins as juveniles, often variegated at reproductive nodes, depressed obovate to shallowly obtriangular to narrowly transversely elliptic, 2(–3)-lobed or ca. truncate, 5(–7)-veined at base, the lateral lobes (acuminate to) acute, often rounded at the very apex, the central lobe retuse to obsolete (or obtuse), the angle between the lateral lobes (75°–)90°–130°(–150°); laminar nectaries (6–)8–16(–28) per leaf, borne 1–12 mm from margin, both proximal (exmedial) to the primary lateral veins and between the primary lateral and central veins. Inflorescence often present to 20 cm long as a condensed terminal shoot with aborted laminae, the petioles and their nectaries still present. Peduncles (1)2 per node, 1–7(–10) mm, uniflorous; bracts absent. Flowers borne vertically, with no detectable odor, light yellowish green, the corona dark violet or purple, apically yellowish; stipe 12–30 mm; hypanthium ca. 6–9 mm diam.; sepals (8–)10–14.5 × 3.5–6.0 mm, narrowly triangular to oblong triangular, outermost two slightly cucullate, with no apical or subapical corni, greenish yellow inside and out, or greenish outside and lightly flushed with reddish purple, reflexed at anthesis so that calyx is open ca. 240°; petals absent; coronal filaments in ca. 5–7(–8) series, the outermost series 8–12 mm long, subequal to sepals, very slender-filiform, reflexed slightly more than the sepals at anthesis, the inner ca. 3–7 series 0.5–3 mm, the three innermost series greatly apically dilated-capitate; operculum represented by vestigial fan-shaped denticles ca. 0.3 mm long; limen 5–6 mm diam., the floor convex, conspicuously glossy brown, dark purple, or reddish purple, with no raised edge; nectary apparently absent; androgynophore absent or present, when present light greenish yellow and unmarked, or purplish at the base or lower ⅓; staminal filaments not connate, or connate 0.5–4.5 mm along androgynophore, the free portions 2.5–3.5 mm long, greenish yellow and not marked, or dark reddish purple; anthers 1.8–3.0 mm long, greenish yellow, not marked, dehiscence extrorse or distal; pollen yellow; ovary 1.9–2.5 × 1.3–2.0 mm, ellipsoid, glabrous; styles 1.5–5.5 mm long including stigmas, light greenish yellow or green, unmarked; stigmas capitate, 1.2–1.9 mm diam. Fruit ovoid. Arils and germination unknown. Chromosome number  $2n = 12$ .

*Distribution and habitat.* Edges, thickets, secondary and primary growth on limestone outcrops or on walls of cenotes, most usually collected on

Mayan ruins or small cliffs, in tropical humid or subdeciduous forest, Yucatan peninsula and adjacent Guatemala and Belize, 100–300 m. It has been found growing with the similar *P. coriacea* at some sites.

*Ethnobotany.* Vernacular names are “Bat wing” (Belize), “Yerba del cuate” (Campeche), “Zodz’ ak” (Yucatán), and most commonly “Xiik zodz” (variously transcribed as “Xig-Sodz,” “Xi’ik so’otz,” “Xiik zotz,” or “Shig sots”) (Yucatán, Campeche). In Belize, “used in a mix to treat pain” (*Hodges & Klassi* 20).

*Passiflora xiikzodz* presents a fundamentally different floral corona from other species in section *Cieca*; furthermore, there is no floral nectary. The corona is highly proliferated, 5–7-seriate instead of 2-seriate, not counting the operculum. Even the operculum is different. While almost all species in the genus have a nectary-cover called an operculum formed by the innermost corona (fused-membranous or not), this protection against rain, useless visitors, and desiccation is lacking in *P. xiikzodz*, the remnants existing only as minute teeth. A floral nectary is absent, and no nectar is formed. The reward for the pollinators is unknown. Pollen might be the reward, but the shiny convex limen is deceptively similar to glistening nectar, and the possibility of attraction by deception should be investigated.

The floral stipe (that portion of the pedicel distal to the articulation) is diagnostically long, 12–30 mm, longer than most other species in the genus. The seeds are unusually elongate for species in section *Cieca* or subgenus *Plectostemma*, being more than two times longer than wide.

The leaves of *P. xiikzodz* are very similar to those of the closely related *P. coriacea*; both are transversely oblong, peltate, with laminar nectaries proximal to the lateral veins, and variegated or not. They are easily distinguished by the position of the large, paired petiolar nectaries. In *P. coriacea* the glands are near the middle of the petiole. In contrast, *P. xiikzodz* has the glands distal or apical on the petiole. The glands are often not visible from above the leaf, being hidden under the base of the blade.

This batwing plant has in its northern populations a variant with a truly unusual flower. The populations around Chichen Itza, Yucatan, have been sampled and grown in the greenhouses; careful study of fresh flowers revealed that the central reproductive structures are shortened and modified so that the flower must dust the pollen on the ventral surface of the pollinators, not on the dorsum as does the southern form. Other differences combine to suggest a cohesive unit recognized here as a separate subspecies.

#### KEY TO THE SUBSPECIES OF *PASSIFLORA XIIKZODZ*

- 1a. Androgynophore 2.6–4.5 mm long; free portions of staminal filaments spreading perpendicular to androgynophore at floral anthesis, the anthers dehiscing proximally, toward corona; styles (including stigmas) 3.5–5.5 mm long ..... *P. xiikzodz* subsp. *xiikzodz*  
 1b. Androgynophore absent or to 1.0 mm long, the ovary sessile or nearly so; free staminal filaments suberect at anthesis, the anthers dehiscing distally, away from the corona; styles (including stigmas) 1.5–2.0 mm long ..... *P. xiikzodz* subsp. *itzensis*

#### ***Passiflora xiikzodz* J. MacDougal subsp. *xiikzodz***

Hypanthium 7–9 mm diam.; staminal filaments connate along androgynophore 2.6–4.5 mm, the androgynophore pale greenish yellow or sometimes purplish brown at base, the free staminal filaments greenish yellow, not marked with purple, reflexing to become perpendicular to the androgynophore at anthesis; anthers extrorse; styles (including stigmas) 3.5–5.5 mm long. Fruit 2.0–3.2 × 1.5–2.2 cm, ovoid, slightly 3-sided, purplish black, estipitate; seeds (4.3–)4.5–5.5 × 1.9–2.3, obcampylotropous, the chalazal beak inclined toward raphe, reticulate-foveate with 13–20(–22) foveae per side. Chromosome number  $2n = 12$ . Figure 2, 4a.

*Paratypes.* BELIZE. COROZAL: Cerros Maya ruins, Lowry’s Bight, coastal area, 8 Apr. 1983, *Crane* 513 (LL); without locality, 1931–1932, *Gentle* 255 (MICH, US). EL CAYO: El Cayo, river bluffs, 15 Feb. 1931 (juvenile and seedling), *Bartlett* 11496a (MICH); El Cayo, 5–13 Mar. 1931, *Bartlett* 12012 (MICH); hillside near Camp 6, 17 Mar. 1938 (fl), *Gentle* 2377 (MICH); Macal River, 20–25 Aug. 1991, *Hodges & Klassi* 20 (MO); ruins of Xunantunich, coll. by J. Turner, *MacDougal* 4677 (MO); ruins of Xunantunich, 17°05’N, 89°08’W, 600–700 ft., 2 Dec. 1968 (fl), *Proctor* 29617 (BM); Panti Trail, Ix Chel Farm, Chaa Creek, 21 Mar. 1990 (fr), *J. Turner s.n.* (MO); 1 mi. NE of Benque Viejo on rd. to Xunantunich, 25 Mar. 1990 (fr), *J. Turner s.n.* (MO). TOLEDO: cliff face, Jacinto Hills, 16°09’N, 88°51’W, 400 ft., 4 Nov. 1933 (fr), *Schipp* 603 (F). GUATEMALA. PETEN: ruins of Uaxactún, 22 Mar. 1931 (fl), *Bartlett* 12270 (MICH); ruins of Uaxactún, 26 Apr. 1931 (fl), *Bartlett* 12755 (MICH); ruins of Temple 1, Tikal National Park, 13 Mar. 1966 (fl), *Contreras* 5578 (F); Santa Elena, on La Libertad road, km 5, 12 Sep. 1966, *Contreras* 6083 (LL); Dos Lagunas, 5 km W on Carmelita road, 6 May 1969, *Contreras* 8478 (LL, MO); Lake Petén Itza, cliff along shore E of San José, 22 Jan. 1962, *Lundell* 17235 (LL); apotal on hilltop, La Cumbre, San Luis area, bordering Arroyo Quebrada Seca, km 122, 28 Mar. 1977, *Lundell & Contreras* 20711 (LL); Plaza Mayor Tikal Ruins, 300 m, 11 Nov. 1967, *Molina* 21075 (EAP, F); Tikal, Parque Nacional, km 16 camino Zococzal a Tikal, 12 Sep. 1969 (fl), *Tún Ortíz* 271 (EAP, F). MEXICO. CAMPECHE: Campo Experimental Forestal Tropical “El Tormento,” km 5 carretera Escárcega a Candelaria, 24 Dec. 1965, *Chav-*

*elas et al. ES-153* (MEXU); ruins of Becán, coll. E. Leiter, cult. at MO 1990–1992, *MacDougal 4690* (MO); Mun. Champotón, a 30 km al N de Calakmul a Escársega, 220 m, 4 Feb. 1983 (fl), *Martínez S. & Téllez 2910* (MEXU). QUINTANA ROO: Kohinlich, July 1974, *Boege 3243bis* (MEXU); 16 km al S de San José de la Montana, sobre el camino a Tomas Garrido, 26 Sep. 1983, *Cabrera & Cabrera 5565* (MEXU, MO); cleared ruin, near Xpujil, 18°10'N, 88°45'W, 300–400 m, 18 Aug. 1974 (fl), *Shepherd 210* (WIS).

The specific epithet, *xiikzodz*, is a compound form of the transliteration of the undeclinable Mayan vernacular name for the plant, meaning “bat-wing.” The epithet is pronounced (more or less) “sheik zoats.” Several other species of plectostemmad passifloras (notably *P. biflora* Lamarck, *P. sexflora* A. L. Jussieu, *P. rovirosae* Killip, and *P. coriacea*) are locally called “ala-murcielago” (Spanish for bat-wing) in northern Mesoamerica, but the shape, texture, and venation of the leaves of this new species particularly suggest a comparison with a bat’s wings. The species is endemic to the region of the Old Mayan Empire, and the vernacular name is well known there (E. Leiter, pers. comm.). Most herbarium specimens examined early by me were inscribed with a different manuscript name which may persist on some sheets; corrected labels have been distributed. The chromosome count was from *MacDougal 4677* (Snow & MacDougal, in press).

***Passiflora xiikzodz* subsp. *itzensis*** J. MacDougal, subsp. nov. TYPE: Mexico. Yucatán: Chichen Itza, [20°40'N, 88°34'W], June–July 1938, *Lundell & Lundell 7470* (holotype, LL; isotypes, LL—2 sheets, MEXU, MICH, US). Figure 3, 4b.

Androgynophorum nullus vel 1.0 mm longum; styli breves, fere sessiles, plus minusve immobiles.

Hypanthium 5.8–7 mm diam.; petals almost always absent (but rarely recorded from occasional sports on cultivated plants as (3.5–)5–7 mm × (1–)2.5 mm); androgynophore absent to ca. 1 mm long, the ovary subsessile within the basally fused or free staminal filaments, the filaments dark reddish purple throughout, suberect at anthesis; anthers dehiscing distally; styles (including stigmas) 1.5–2.0 mm long; immature fruit ovoid, otherwise unknown; seeds unknown. Chromosome number  $2n = 12$ .

*Additional specimens examined.* MEXICO. YUCATAN: Progreso, 1934, *Flores 2* (F); Lake Chichankanab, [19°54'N, 88°46'W], Apr. 1917, *Gaumer 23714* (F); without further locality, 1917–1921, *Gaumer 24415* in part (F, G, MO); Chichen Itza, near Pisté, [20°40'N, 88°34'W], June–July 1938 (fl), *Lundell & Lundell 7375*

(MICH); Chichen Itza, June–July 1938 (fl), *Lundell 7439* (MICH); Chichen Itza, coll. by Dzib Dzib & Leiter, cultivated at MO 1989–1992, *MacDougal 4633* (MO).

The androgynophore in this distinct subspecies is reduced to nearly nothing, the ovary thus subsessile and surrounded by five nearly free stamen filaments thrusting upwards. The presence of a distinct androgynophore is usually considered a generic character in this family, but other species of *Passiflora* have been described with a similarly reduced or absent column (cf. *P. apoda* Harms, *P. multiflora* Linnaeus, *P. ursina* Killip & Cuatrecasas, and *P. monadelphica* Jørgensen & Holm-Nielsen). The anthers in *P. xiikzodz* subsp. *itzensis* differ by not flipping over to an extrorse position after the flower buds open, but instead moving only slightly from the original introrse position to dehisce distally (upwards), away from the corona. The stigmas are nearly sessile on short nonmoving styles, with their receptive surfaces also directed distally. The pollen is thus dusted on the ventral surface of any insect visitor that might walk on the flower. Although pollinators of neither subspecies are known, relatives are hymenopteran-pollinated (sect. *Cieca*, Lindman, 1906; *P. coriacea*, J. Turner, pers. comm.). The difference in placement of pollen between the two subspecies may indicate differences in pollinators, but this remains unknown.

Petals appeared in a few flowers of the cultivated *MacDougal 4633* in October of 1989 and 1991. These were well formed but small, and their occurrence is an anomaly in the otherwise apetalous section *Cieca*.

Both subspecies appear to be self-incompatible. More than 60 artificial self-pollinations of clones of both subspecies proved unsuccessful in the greenhouses, and no fruits have been produced by autogamy in two years of cultivation. Viable seeds were produced easily between two clones of subspecies *xiikzodz* (*MacDougal 4690, 4677*) and even subspecies *xiikzodz* and *P. coriacea*, with hybrids grown to flowering. The hybrids with *P. coriacea* (*MacDougal 4678*) had normal-looking, intermediate flowers with abundant pollen; pollen viability or stainability has not been examined.

Artificial cross-pollinations in the greenhouse between the two subspecies has proved unsuccessful. About 15 crosses in both directions between *MacDougal 4633* and *4677* have been tried, with aborted fruits with no viable seed formed with *4677* as the pollen donor, and with no fruits formed with *4633* as the pollen donor. The lack of fertility between the two subspecies underscores the divergence of the taxa, but more information would be needed to support the recognition of two separate species.

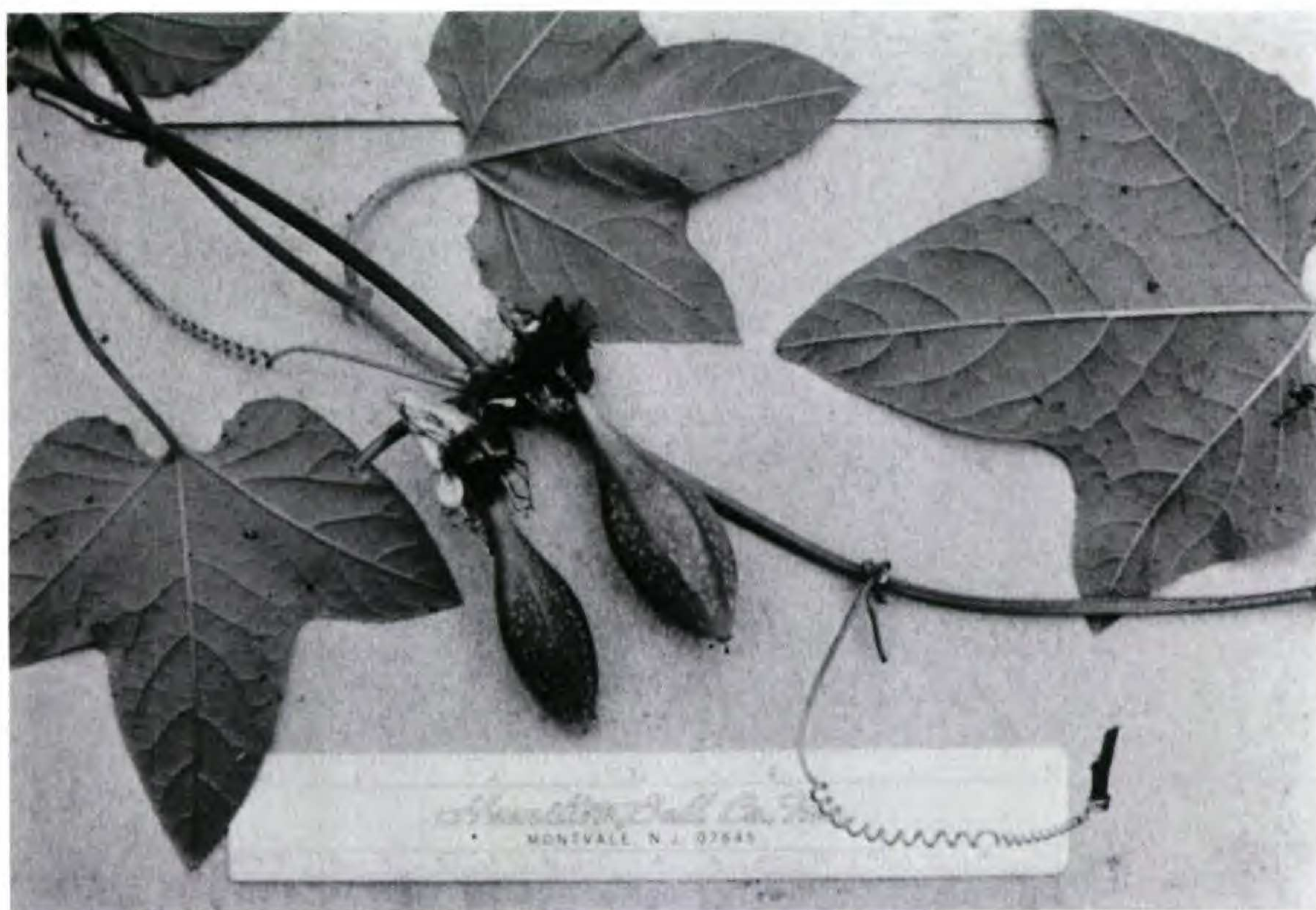


Figure 5. *Passiflora oxacensis* J. MacDougal, with immature fruit (*MacDougal* 329). White ruler is 16.2 cm long.

The flowers of both variants of *P. xikzodz* look similar from a distance, although the northern type is smaller, and both have the same unique, convex, shiny limen with modified operculum and proliferation of coronal rows.

The specimens collected by both Flores and Gaumer cited above are tentatively included in this subspecies due to their geographic position at the north of the range, but the specimens are sterile. The chromosome count was from *MacDougal* 4633 (Snow & MacDougal, in press).

***Passiflora oxacensis*** J. MacDougal, sp. nov.

TYPE: Mexico. Oaxaca: Distr. Miahuatlán, 1 km N of [San José de] El Pacífico, or 34 km S of Miahuatlán on Hwy. 175 at Km 132, 16°05'N, 96°30'W, ca. 2,500 m, 26 July 1965, *Roe, Roe & Mori* 616 (holotype, WIS; photographs, DUKE, MEXU; isotypes, DUKE, ENCB, F). Figure 5.

*Passiflora* ad sectionem *Pseudodysosmiam* pertinens, scandens, pubescens trichomatis uncinatis; petioli duo glandulis sessilibus infra medium instructi; folia trilobata, basi cordata et denticulata, lobis acute vel acuminate triangularis; bracteae lineares vel setaceae; coronae filamenta uniseriata vel biseriata, filamentis exterioribus 11–14 mm longis; operculum plicatum; ovarium glabrum; arillus rubroaurantiacus; semina reticulatim foveata.

Climbing vine 1.5–3 m with stems apparently annual from slightly thickened perennial roots, sparsely pubescent throughout with 0.25–0.60-mm-long uncinuate trichomes; stem subterete and slightly

striate to subangulate. Stipules 8–14 × 4–8 mm, ovate-auriculate and apiculate to long caudate, the margins entire and ciliolate; petioles 2.8–6 cm, 2-glandular 0.25–0.50 the distance to the apex, the nectaries 1.0–2.0 mm total length, 1.0–1.8 mm diam., paired or subopposite, pyriform or hemispherical, sessile to short-stipitate; laminae (5.5–)7–14 × (6.5–)8–15.5 cm, never variegated, 3-lobed 0.30–0.40 (–0.45) the distance to the cordate base, the lobes triangular and acute to nearly acuminate, the central lobe not narrowed at base, the angle between the lateral lobes 85°–110°(–117)°, ratio of lateral to central lobe lengths (0.65–)0.70–0.83, margins proximal to lateral lobes denticulate with 5–8(–10) teeth per lobe, margins distal to lateral lobes entire; laminar nectaries 0.5–0.9 mm diam., 2–3 per sinus, very rarely 1–2 also proximal to lateral lobes, 1.5–6(–9.0) mm from margin, sessile; juvenile leaves more shallowly lobed, 0.10–0.30 the distance to the base, the lobes with convex margins forming a terminal angle of ca. 90°. Peduncles (1)2 per node, 2.0–2.5 cm; bracts (2.6–)3.0–6.5 × 0.15–0.5 mm, linear-triangular to capillary, entire. Flowers 4–5 cm diam., oriented sublaterally but below horizontal, with a pleasant flowery-sweet odor, open and receptive from morning to midday; stipe 0.8–2.5 mm; hypanthium 12–15 (–18) mm diam., conspicuously concave abaxially at junction of stipe; sepals 15–21 × 7–10 mm, ovate-triangular and acuminate, ecoriulate or cori 1–2 mm long, pale yellowish green to greenish white and puberulent abaxially, pale yellowish green

to whitish adaxially; petals 6–7 × 4.5–5.0 mm, (widely) ovate, white; coronal filaments in 1 main series, sometimes with a vestigial second series, the outer filaments ca. 52–56, 11–14 mm long, whitish to cream and sometimes becoming light yellow distally, violet or purplish at base and with 1–3 violet bands 4–9 mm from base, giving the appearance of 2–3 violet rings, or the upper bands sometimes splotchy and run together as one pale indistinct band; inner coronal filaments (if present) 0.25–0.75 mm long, submicroscopic and inconspicuous, capilliform to clavate, generally occurring alternate with the outer filaments, expressed mainly in the sepal sectors, usually absent in the petal sectors, white, purplish at base; operculum 1.6–2.2 mm, whitish or usually whitish with purple streaks near base; limen white or white with purple speckling; staminal filaments connate 6.0–7.0 mm along androgynophore, the free portions 5.5 mm long, very lightly speckled with reddish brown (dried); anthers 3.9–5.0 mm long, the connective speckled with reddish brown at its abaxial proximal end (dried); ovary 4.5–6.3 × 2.1–2.8 mm, ellipsoid, borne on a 0.8–2.0 mm long stipe, glabrous; styles 7–8 mm including stigmas; stigmas 2.0–2.5 mm diam. Fruit 6.0–8.0 cm long including 1.5–2 cm stipe, 2.8–3.0 cm diam., ovoid-ellipsoid, ellipsoid, or slightly obovoid, apically abruptly and bluntly conical, sometimes also with an abrupt nipple, purplish black with white bloom, often light greenish yellow proximally and on stipe; arils ca. 8–9 mm long, medium to very orange, fimbriate at apex, fruity-sour tasting; seeds 4.5–5.0 × 3.0–3.5 mm, obovate to widely obovate, coarsely reticulate-foveate with (15–)16–20 foveae per side; germination epigeal. Chromosome number  $2n = 12$ .

*Distribution and habitat.* Known only from several populations near the road over the crest of the Sierra de Miahuatlán of Oaxaca, Mexico, in moist to wet forest at the lower edge of the pine zone, 2,400–2,500 m. *Passiflora oaxacensis* is found on steep slopes in open pine woods, forest edges, disturbed areas, or roadside thickets, climbing herbs, shrubs, and dead branches of tree falls. The forest contains a small amount of oak, and herbs such as *Maianthemum* Wiggers are common. This locality is in an area classified as “húmedo, semifrío,” with 1,200–1,500 mm of rain annually and an average annual temperature of ca. 12°C (CETENAL, 1970). This climate type has a restricted distribution in Oaxaca but extends roughly 40 km eastward from San José del Pacífico, with two or three small isolated patches to the west. *Passiflora oaxacensis*, or a close relative, may thus be on other nearby peaks.

*Paratypes.* MEXICO. OAXACA: W-facing slope, 1.0 mi. N of San José del Pacífico, Distr. Miahuatlán, ca. 7,800 ft., *MacDougal* 329 (CHAPA, DUKE); rootstocks of *MacDougal* 329 cultivated at Duke University 1979–1980, *MacDougal* 329GR (CHAPA, DUKE, MEXU); Puerto del Pacífico, *Lau* s.n. in 1987 (photographs: DUKE); cultivated at the Missouri Botanical Garden 1988–1992 from seeds from *Lau* s.n. in 1987, *MacDougal* 3009 (BM, MEXU, MO).

*Passiflora oaxacensis* belongs in subgenus *Plectostemma* sect. *Pseudodysosmia* (Harms) Killip on account of the plicate operculum, basally serrate leaves, one main filamentous coronal row, large stipitate purple fruit with orange pulp, circinnate development of the tendrils at the shoot apex, and the unciniate trichomes. The species is similar to *P. sicyoides* Schlechtendal & Chamisso, from which it may be distinguished vegetatively by having larger stipules, sessile petiolar nectaries, angles between the lateral laminar lobes of usually less than 110° compared to usually more than 110°, ratios of lateral to central lobe lengths usually 0.70–0.80 compared to 0.53–0.75, and 10–20 laminar marginal teeth compared to less than 12. Fertile material differs notably by the longer outer coronal filaments 11–14 mm long compared to 4–8(–10) mm long, which number 52–55 compared to 59–65(–70), by having fruits more ovoid than obovoid, and seeds with fewer testal foveae. Additionally, *P. sicyoides* often has peduncles that exceed 30 mm.

A second, vestigial but numerous inner row of coronal filaments is seen in two of the three collections. Other species of this section sometimes have flowers with a few vestigial inner filaments, but here the filaments are numerous although diminutive and doubtless nonfunctional in the reproduction of the plant.

The chromosome count was made from *MacDougal* 3009 (Snow & MacDougal, in press). Clones *MacDougal* 329GR and *MacDougal* 3009 were self-incompatible in the greenhouse, based on more than 20 controlled self-pollinations.

This species is named for the State of Oaxaca, Mexico, where it appears to be restricted to a small area.

***Passiflora escobariana* J. MacDougal, sp. nov.**

TYPE: Colombia. Antioquia: Mun. de Frontino, road between Nutibarra and La Blanquita, region of Murri, ca. 24.5 km from Nutibarra, 1,090 m, 8 Feb. 1991, *J. MacDougal*, *D. Restrepo* & *D. S. Sylva* 3823 (holotype, HUA; isotypes BM, COL, CR, HUA, MEDEL, MO, US). Figure 6.

*Passiflora* ad sectionem *Xerogonam* pertinens; caulis sub3–5-angularis, vinosus; folia 7–25 cm longa, 6–12



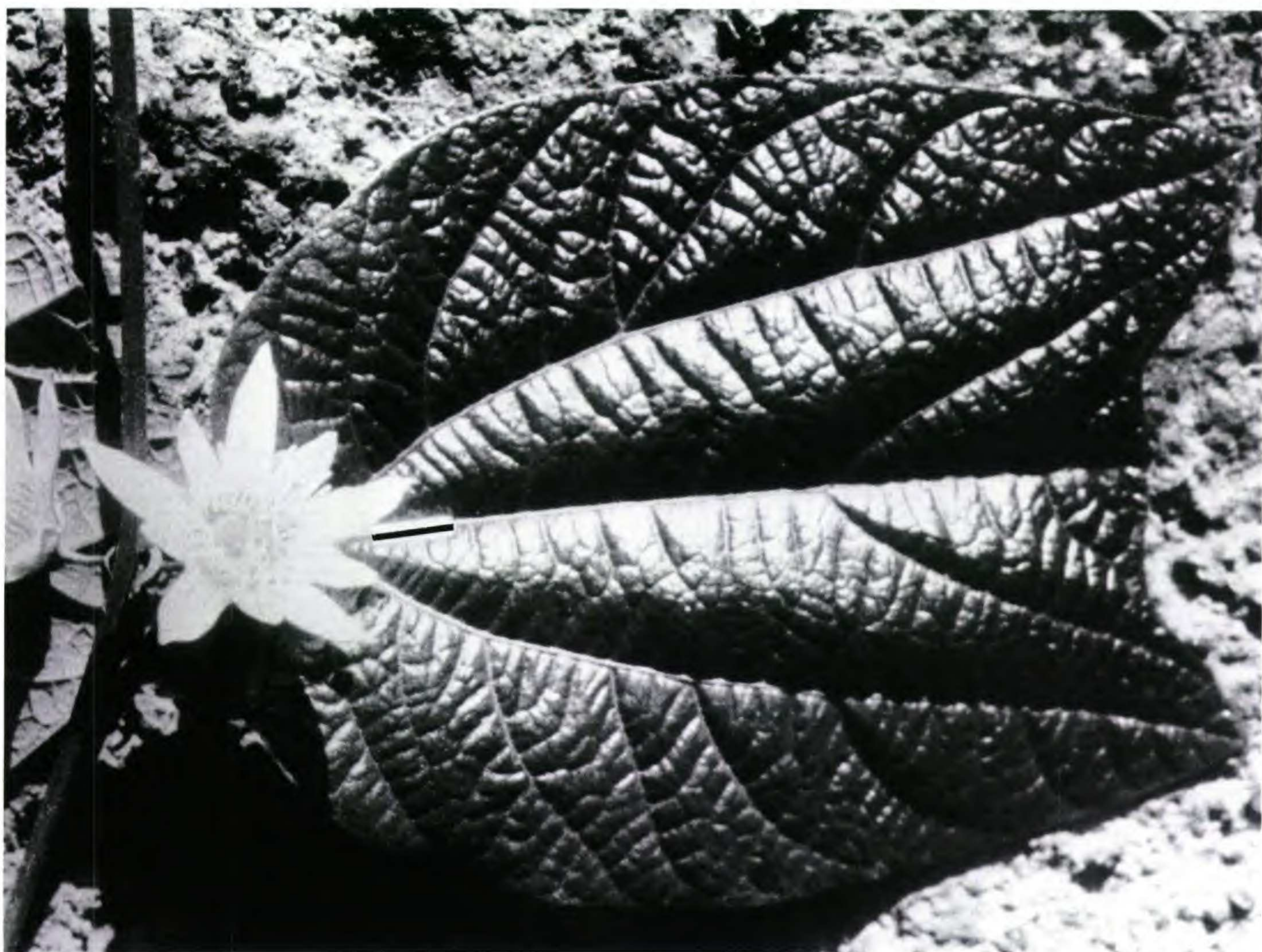


Figure 6. *Passiflora escobariana* J. MacDougal, flowers closing (MacDougal et al. 3823GR). Scale bar on midrib of leaf is 1 cm.

lata, eglandulosa nonprofunda bilobata, lobis acutis vel obtusis, marginibus integris, trichomatibus adaxialibus minus quam 0.8 mm longis; pedunculi ebracteati; sepala 15–23 mm longa, 4.5–9 mm lata; coronae filamenta 1–2-seriata, filamentis exterioribus 10–13 mm longis, candidis vel eburneis, parte inferiore roseis; operculum plicatum; androgynophorum 7.0–9.5 mm longum; ovarium minute dense puberulens; capsula fusiformis 6-valvata, carinis rubris.

Vine 5–10 m, minutely puberulent throughout at the shoot tip with 0.04–0.25 mm long antrorsely appressed trichomes. Stems ca. 3–5-angular above, obscurely so below, reddish, puberulent. Stipules 5–7 × 0.5–0.7 mm, linear-triangular or slightly falcate; petioles eglandular, 2.5–6 cm long; laminae 7–25 × 6–12 cm, 2(3)-lobed 0.11–0.20(–0.27) the distance to the shallowly cordate base, with the central lobe always shortest, entire, not variegated, somewhat bullate, adaxially sparsely but evenly pubescent or hirsutellous with straight 0.10–0.5 (–0.8) mm long trichomes, abaxially lightly and evenly pubescent with 0.2–0.3 mm trichomes, the lateral lobes acute to acuminate, the central lobe obtuse, the angle between the lateral lobes 33°–50°; laminar nectaries absent. Older stems cauliflorous,

the inflorescence a condensed leafless axillary shoot 1.5–3.5 cm. Peduncles (1)2 per node, (5–)7–26 mm, uniflorous, red; bracts absent. Flowers creamy-white tinged pink, with a reddish center, borne ± upwards, with a mild sweet odor, open from mid-morning to just after midday; stipe (2.5–)4–8 mm (to 12 mm in fruit); hypanthium 10–13 mm diam., very pale greenish or nearly white, sometimes slightly tinged with pink. Sepals (15–)18–23 × (4.5–)6–8(–9.0) mm, narrowly triangular or oblong-triangular, acute, strongly 3-nerved, with no apical projection, whitish, cream, or pale green abaxially, whitish adaxially and sometimes tinged pink or red on the basal part and edges; petals (11–)13–17 × 4.0–5.5 mm, narrowly ovate to broadly lanceolate, acute but the very tip rounded, (whitish to) pale pink; coronal filaments in 1 or 2 series, the outer ca. 27–29 in number (N = 2), 10–13 mm long, filiform, the basal portion forming a bowl, the tips spread about 180°, the filaments white in the lower half, pale yellow in the upper half, marked reddish purple adaxially in the lower 2/5; inner corona present and numerous in the flowers of some branches of the type clone but absent in others, absent or only a

few vestigial filaments seen in paratype, 2–3 mm long, capillary, purplish distally, with paler apex; operculum 2.0–3.0 mm long, membranous, plicate, light purple; limen 6–7 mm diam., concave-shallowly funnellform at insertion of androgynophore, very pale greenish yellow, not marked with purple; nectar ring 1 mm high, conspicuously closer to limen edge than base of operculum; staminal filaments connate 7.0–9.5 mm along androgynophore, light greenish yellow at base, paler distally, not marked with purple, the free portions ca. 4 mm long; anthers 3.0–4.8 mm long, not marked with purple, with pale to light yellow pollen; ovary 2.0–4.5 × 1.2–3.0 mm, ellipsoid, 6-ridged, finely and densely (microscopically) puberulent, pink or pale purplish red, or pale yellowish green; styles 5–6 mm long including stigmas, reddish (especially distally); stigmas ca. 2 mm diam., capitate, green. Fruit 7.0 × 2.5 cm, fusiform, 6-ridged, dehiscent, red on ridges, cream between ridges; arils, seeds, and germination type unknown. Chromosome number  $2n = 12$ .

*Distribution and habitat.* Known only from the Colombian type and one collection in adjacent Panama, *Passiflora escobariana* is from primary lowland and premontane rainforest, in small to medium-sized trees at edges of light gaps.

*Paratypes.* COLOMBIA. ANTIOQUIA: cuttings from type collection grown 1989–1992 at Missouri Botanical Garden, *MacDougal et al.* 3823GR (HUA, MO). PANAMA. DARIEN: Parque Nacional Darién, Estación Pirre, a orillas del Río Perresénico entre la Estación Pirre y la cascada, 8°00'N, 77°45'W, 150 m, 10 Oct. 1990 (fl), *H. Herrera* 720 (BM, MO, PMA).

*Passiflora escobariana* is assigned to subgenus *Plectostemma* sect. *Xerogona* (Rafinesque) Killip on account of the plicate floral operculum, lack of extrafloral nectaries, lack of bracts, and dehiscent carinate fruit. It is most similar to *P. rovirosae* and *P. costaricensis* Killip, and shares with them the tendency to form leafless flowering axillary shortshoots. The stem of *P. costaricensis* is always sharply triangular, even 3-winged, and the upper surface of the leaf is hirsute with most trichomes longer than 1 mm; the new species has sub3-, 4-, or 5-angular stems, and the leaves are not hirsute. *Passiflora rovirosae*, from southeastern Mexico to northern Guatemala and Belize, is most similar but has narrower, more densely pubescent, nonbullate leaves with a lateral lobe angle of 22°–30°(–40°), and yellow flowers with a well-developed inner coronal row.

A clone from the type collection was grown in the greenhouses where it flowered a few times a year (mainly in the winter). The species may be self-

incompatible: ten controlled self-pollinations failed to set fruit, and no fruit has been produced by autogamy in four years of cultivation. The chromosome count was from *MacDougal et al.* 3823GR (Snow & MacDougal, in press).

The paratype, from Panama, differs from the type in its 4–5-angular stem instead of sub3–4-angular, in having notably longer petioles (4–6 cm vs. 2.5–3.5 cm), and longer trichomes on the upper surface of the leaf (0.2–0.8 mm vs. 0.10–0.25 mm).

It is a privilege to name this passionflower in honor of Linda Albert de Escobar, eminent student of passionflowers, whose valuable work in the genus and on the flora of Colombia is well known.

*Acknowledgments.* I thank Eldon Leiter for his dogged pursuit and collection of live material of *P. xikzodz*; his help alone is responsible for most of our understanding of this species. I am also indebted to Joanna Turner for her photographs, observations, and live material of that species from Belize. Victoria Bricker and Anne Bradburn at Tulane University guided the transliteration of the Mayan epithet. Alfred Lau generously collected seed of *P. oaxacensis*, Melvin Turner assisted with *P. juliana*, and Kathy Upton cared for all four of the new taxa in the greenhouse. I thank my Colombian colleagues Diego Restrepo and D. Stella Sylva for guidance during fieldwork in Antioquia, and the curators of the listed herbaria. The Latin diagnoses were graciously polished by Henk van der Werff and William L. Culberson. The initial research on three of these species and fieldwork in Mexico was accomplished during graduate studies at Duke University under a National Science Foundation Fellowship, further supported by NSF grant DEB-7912607.

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